Population biology of the subterranean rodent *Ctenomys australis* (Tuco-tuco) in a coastal dunefield in Argentina

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Abstract

The population biology of the subterranean rodent *Ctenomys australis*, tuco-tuco, was studied along a coastal dunefield. Average density was 16.1 ind./ha during the studied period and the animals showed a random spatial distribution pattern. The breeding season lasted the entire year determining a lack of a discrete period of recruitment and a complex age structure. Overall sex ratio was skewed towards females, whereas that for young individuals was even. Females reached sexual maturation before males and brought only one litter to the population in the year they were born. During summer, females showed overlap between pregnancy and lactation demonstrating the existence of a post partum estrus. Mean litter size was 2.9, in which litter size from post partum estrus was lower than that corresponding to the first pregnancy. Adult animals were sexually dimorphic both in weight and length. Males presented low relative testes length. Dispersal happened above-ground. Mean monthly recovery percentage was 19%. Group of colonizers was composed predominantly by immature animals. No differences were found concerning sex ratio, age structure, and litter size between dispersers and residents.

Key words: *Ctenomys australis*, population biology, dispersal, subterranean rodents

Introduction

The distribution of *Ctenomys* rodents covers a large area of South America, extending from 17 °S to 54 °S latitude and from the Andes to the Atlantic Ocean. Within this area they occur in a wide variety of habitats. This habitat versatility is indeed a reflection of the subterranean way of life, as the permanent plugged burrows insure microclimatic conditions of both humidity and temperature relatively independent of the exterior ambient conditions (Rosenmann 1959). Nonetheless, a more detailed study of their distribution showed that tuco-tucos are prone to live in sandy soils or at least in well-drained ones (Contreras 1973). This is not only due to digging but to metabolic constraints related to heat storage and respiratory gas exchange (McNab 1966). As a consequence of its size, *C. australis* occupies looser, more friable soils than smaller species (Vleck 1979; Busch 1989; Contreras and McNab 1990). This fact conditioned their distribution, which is restricted to the southern coastal region of Buenos Aires province from Necochea to Bahia Blanca in a sandy dunebelt close to the beach.

C. australis shows individual territoriality. They perform most of their dairy activities in permanently sealed burrow systems, making only brief surface excursions for collecting

plant material. Thus, the burrow system plus a narrow surface periphery compose the exclusive territory for each individual. This particular way of life coupled to little success with rearing individuals of this species under conditions of captivity, make it difficult to obtain ecological data.

The aim of the present study is to provide information about life history traits on one species dwelling underground. This will be useful in terms of finding possible interpretations for the extraordinary specific diversification undergone by this genus (Reig et al. 1990) in contrast to what is found in other genera that share the same way of life. Furthermore, since *C. australis* is restricted to natural grasslands over sand dunes, which are considered as vulnerable habitats, this rodent warrants special conservation status for which knowledge of its biology would be useful.

Material and methods

Study area

The study was conducted 10 km south of Necochea, Buenos Aires, Argentina. It consists of a 4–10 km wide coastal dune fringe which slopes into the inland natural grassland. Sand dunes reach altitudes ranging from 30 to 50 m above sea level, and extend 200 to 2 000 m (Frenguelli 1928). The natural grassland over the dunes exhibits a vegetation cover of about 20%, with dominant plants including *Poa* sp., *Panicum racemosum*, and *Calistelgia soldanella* (Malizia et al. 1991).

Data collection and analysis

Individuals of *C. australis* were collected in six trapping periods from May 1991 to May 1992. In each sampling period, which extended over 5 days, the capture area was placed along a coastal dune fringe nearly 1 km far away from that corresponding to the previous ones. Such an arrangement was chosen both not to perturb the population and to minimize the effect of producing vacant areas in our results. The fact that *C. australis* individuals restrain their activities to their burrow system and are highly sensitive to handling, makes it extremely difficult to implement mark-recapture programs. This situation led us to implement a removal method. To perform the trappings, snap-traps Oneida Victor N° 0 (without any kind of bait) were located at the entrance of the burrows to catch all individuals present in each removal area which averaged 0.80 ha in size (range 0.50–1.25 ha). Edge effects leading to possible counting errors were eliminated by considering exclusively the individuals that have all the tunnel openings (commonly used for foraging activities) inside the removal area. The traps were checked hourly during daylight hours and closed during the night. Position of capture was recorded to determine spatial distribution. In spite of the recognized limitations of data coming from removal of all animals occupying an area, it constitutes the only way to obtain ecological information for this species. On the other hand, this methodology allows to obtain detailed information of the reproductive status of individuals.

Body weights and linear measurements were taken at death and reproductive condition was obtained by autopsy. Immature females were characterized by presence of filiform uterus, closed vagina, and no follicular activity whereas subadult females presented follicular activity. Reproductive individuals showed an open or plugged vagina, ripe follicles, placental scars, signs of pregnancy or postpartum pregnancy. Males with spermatozoa in epididymis were classified as mature. Ossification of humeri was used to determine six relative age classes. All reproductive and age criteria were taken from Pearson et al. (1968) and Malizia and Busch (1990). These data provided information about density, spatial distribution pattern, reproductive activity, and age structure of the resident population.

To assess dispersion of *C. australis*, two experimental plots 3 km apart, one 1.44 ha (S plot) and another 0.77 ha (N plot) were delimited and all the tuco-tucos present inside the plots were removed. No mound building activities were detected once removal was concluded. Individuals that subsequently colonized these previously vacated areas were removed from July 1992 to May 1993 (S plot) and from September 1992 to May 1993 (N plot). These individuals were considered as dispersers in this study. Those individuals living close to the edges of the experimental plots that could have moved underground simply by extending their burrow systems were not included in our analysis. We easily recog-

nized them since they were initially marked. Dispersal individuals were autopsied and the same data registered as for residents.

Results are given as X ± SE. The T-square distance method was used to analyse the spatial pattern of populations found continuously across the grassland (Ludwig and Reynolds 1988). Chi-square tests were used to determine whether sex ratio deviated from parity. Non parametric Kruskall-Wallis tests were used to compare differences between litter size from first and second pregnancy and between residents and dispersers. Differences in body mass and length between males and females were tested using t-test. Chi-square contingency table analysis was used to test independence between sex and condition of animals (residents or dispersers); similarly was tested whether relative frequencies of animals of each reproductive condition were the same for residents and dispersers.

Results

Density and spatial distribution

Average density was 16.1 ± 1.1 ind./ha during the study period. Densities in samples were 20 ind./ha (May/1991), 17.2 ind./ha (August), 10 ind./ha (October), 14.4 ind./ha (December), 26.7 (March/1992), 8.0 ind./ha (May), 10.0 ind./ha (July). These records come from removal areas of 0.80 ha average in size (range 0.5–1.25 ha). In computing densities, juvenile individuals sharing the maternal burrow were not considered, whereas non captured individuals which presented clearly mound-building activity were scored.

Indices derived from distances between points and individuals in arbitrary sampling units were used for spatial pattern analysis. Table 1 shows average distances between points and individuals and spatial patterning indexes for each sampling period. The distribution of *C. australis* was random. Both z values for Spatial Pattern Index (C) and Johnson and Zimmer Index of Dispersion (I; Ludwig and Reynolds 1988) were lower than the critical values for each sampling period. Thus, we accepted the hypothesis that the distances were measured between points and individuals within an underlying random pattern.

Table 1. Mean distance between individuals and random points used to calculate spatial patterning indexes for *Ctenomys australis* from Necochea.

Mean distance (m)	Sample					
	May	Aug	Oct	Dec	Mar	May
Point-nearest individual	13.3	11.25	22.24	13.06	12.76	20.69
Individual-nearest neighbor	18.53	21.76	41.06	29.28	16.45	37.16
Spatial pattern Index (C)	0.49	0.40	0.52	0.43	0.58	0.40
z statistic	−0.15	−1.83	0.30	−1.34	1.54	−1.86
Dispersion Index (I)	2.30	2.18	2.11	1.72	1.76	1.85
z statistic	0.92	0.55	0.32	−0.85	−0.72	−0.45

z (crit) = 1.96   P = 0.05

Sex ratio

Since numbers from each sample were in general too small to perform valid statistical tests, the data were grouped and tested for overall differences.

The sex ratio of younger individuals (relative age class i, n = 26) was nearly even (1 male: 0.75 female; $X^2 = 0.57$, df = 1, P > 0.05) but the adult sex ratio (n = 50) was heavily skewed toward females (1 male: 2.125 females; $X^2 = 6.48$, df = 1, P = 0.011).

Age and maturation

To characterize the individuals belonging to the six relative age classes that resulted by ranking the epiphyseal ossification of humeri, data provided by autopsy plus that obtained from animals reared in captivity were used.

Individuals belonging to age class i were captured at the same location as the mother or close to her. For this reason they were not considered as residents. Mean body weight was 119.3 ± 38.7 g and 118.1 ± 28.3 g for males and females, respectively. These animals can be attributed to a chronologic age of 0 to 3 months. Smaller individuals of this group were sucklings.

Those individuals of age class ii were captured in their own tunnel system. All males had no spermatozoa in their epididymis and their mean body weight was 236 ± 74.4 g. Females had experienced follicular activity and a mean body weight of 216 ± 49.6 g. We estimated a chronologic age around 3 to 6 months for this group.

Males of age class iii (mean body weight = 264.9 ± 5.9 g) were all mature and most of the females (mean body weight = 261.7 ± 58.1 g) presented signs of pregnancy; all were between 6 to 9 months old.

At age class iv, the mean body weight was 327.1 ± 62.7 g and 268 ± 48.5 g for males and females, respectively. Females were pregnant or showed signs of previous pregnancies. The age of these animals was estimated to be 9 to 12 months.

Males of age class v weighted 330 ± 93.2 g and females 324 ± 38.5 g. Males from age class vi showed no evidences of senility since all of them presented spermatozoa in their epididymis (mean body weight = 416.5 ± 54.3 g). The only female captured belonging to this age class weighted 334 g. For the two later age classes no chronologic age could be assigned.

Reproduction

Considering the breeding period as the time during which females are pregnant, it can be inferred that *C. australis* has a continuous one. Once sexual maturation is attained in either sex, the animal remains in reproductive activity for the entire year round (Figs. 1 a, b). Pregnant females were scored throughout the entire year and since they attain maturity nearly at six months of age, they brought only one litter to the population in the year they were born. During summer (December and March samples) females showed overlapping between pregnancy and lactation, evidencing the existence of a post partum estrous.

For *C. australis*, information concerning longevity and length of gestation period is unavailable, nonetheless we can estimate that the females could produce three or four litters in their life span considering that for *C. talarum* these values were calculated as 2 years and 102 days, respectively (Busch et al. 1989; Weir 1974).

Litter size

Mean litter size (determined by embryo counts, which could slightly overestimate litter size at birth) was 2.9 ± 1.37 (n = 20). Nonetheless, if we compare the litter size from the first and second pregnancies (the last one produced as a result of a post partum estrous), we found an interesting difference. The second litter was smaller than the first one (1.85 ± 1.07, n = 7 and 3.46 ± 1.19, n = 13, respectively; U crit = 76.5, df = 1, P < 0.01). Furthermore, females both during lactation and pregnancy showed a high incidence of pre- and postimplantation embryo losses, as evidenced both from no matching between number of corpora lutea and embryos and clear resorbtion of embryos.
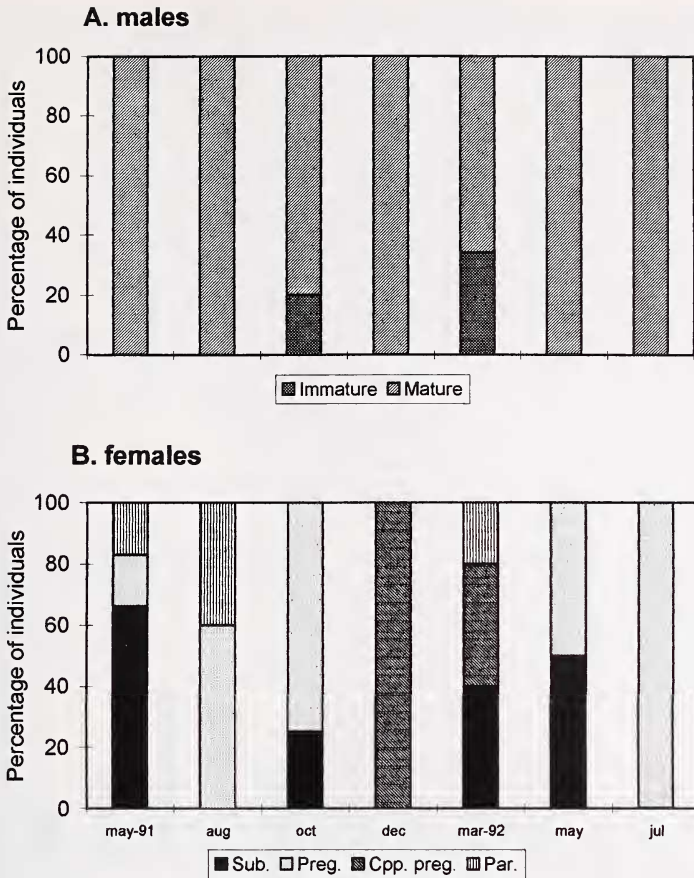
A. males

B. females

Fig. 1 a) Proportion of mature and immature male individuals of *Ctenomys australis*; b) Proportion of reproductive (par = parous, cpp. preg. = pregnant and lactating, preg = pregnant) and non-reproductive (sub. = subadult, imm = immature) female individuals of *Ctenomys australis*.

Sexual size dimorphism and relative testes size

Adult individuals of *C. australis* show a clear sexual size dimorphism, i.e. males being larger than females. Frequency distribution analysis (Fig. 2) and male: female ratio indicate the existence of a more pronounced dimorphism in mass than in length. Ratio of dimorphism in weight was 1.3 with a mean weight of 367 ± 69.2 g (n = 32) for males and 288 ± 50.1 g (n = 43) for females (t = 5.64, P < 0.01), while the ratio in length was 1.1 and mean length of 221 ± 15.1 mm (n = 32) for males and 206 ± 12.9 mm (n = 43) for females (t = 4.28, P < 0.01). Relative testes size (testis/body length) was 0.054 ± 0.007 (n = 30).

Dispersal

During the study period, 54 individuals colonized previously vacated areas by above-ground (30 animals for S plot and 24 for N plot). Both areas remained without animals at the first sampling period, showing with certainty that all the tucos had been effectively removed. Subsequent occupation was performed using old tunnel systems, as evidenced by location of the animals in the field.
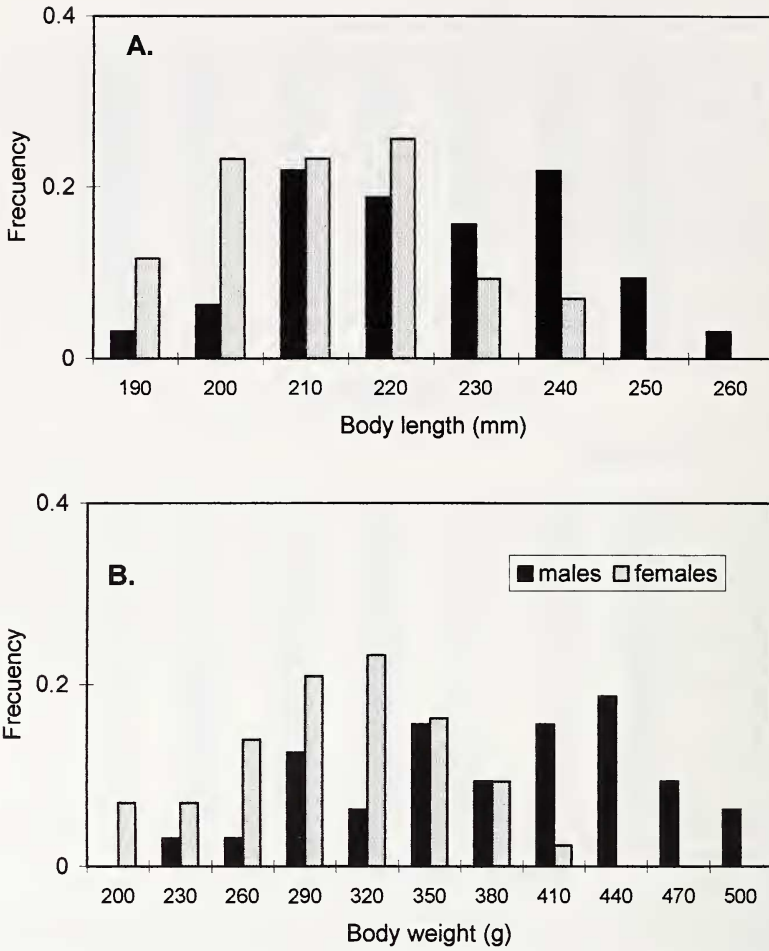
Fig. 2. Frequency distribution of body length (A) and body weight (B) of *Ctenomys australis.*
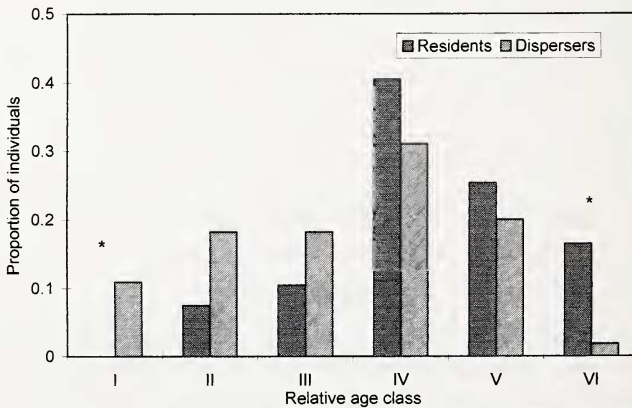

Fig. 3. Proportion of resident and disperser individuals of *Ctenomys australis* (both sexes pooled) for each relative age class.

Mean monthly recovery percentage (number of colonizers removed from the experimental plot at time t/resident population size at the same time $\times 100$) was 10.8% (range 0–20%) for the S plot and 27.0% (range 0–65%) for the N plot, with a general average around 19%.

Due to sample size, we pooled data coming from the two experimental plots in the analysis of residents versus dispersers. The group of colonizers was composed by the same proportion of both sexes (1 male: 1.25 female, $X^2 = 0.66$, df = 1, P = 0.417). Although the resident population showed a clear skew towards females, dispersers and residents did not differ significantly ($X^2 = 1.69$, df = 1, P = 0.194).

Reproductive activity and dispersal proved to be dependent attributes for both sexes (females: $X^2 = 5.19$, df = 1, P = 0.023; males: $X^2 = 7.18$, df = 1, P = 0.007). Representation of reproductive individuals was higher for male and female resident population than for dispersers. Resident males were mostly reproductive (90.8%, n = 21), whereas for dispersers this proportion was only 54% (n = 24). Likewise, reproductive females represented 75% (n = 40) for residents and 48.4% (n = 29) for dispersers. In addition, 40% of non-reproductive female dispersers were subadults with follicular activity. Pregnant females also dispersed. Their mean embryo counts were 3.7 ± 0.63 (n = 13) and did not differ from that belonging to general mean litter size and first pregnancy for residents (U = 99, P = 0.23 and U = 81, P = 0.84, respectively).

The age composition of dispersers did not differ significantly from that of residents. Comparisons of the percentage of dispersers versus that of the residents for each relative age class showed that only the extremes of the age distribution differed (Fig. 3). We found no resident individuals of age class i and few animals of age class vi participating in the dispersal process ($z_{obs} = 3.7$ and 3.09 respectively, $z_{crit} = 1.96$, P < 0.05).

Discussion

In contrast to voles, the mammalian r-strategist par excellence, which possess a high capacity to expand their numbers in transient habitats and produce large litters during gestation periods comprising few weeks by early reproductive females, *C. australis* as other *Ctenomys* populations is a relatively K-selected group of rodents. They breed later, develop slower, are more stable in numbers and have fewer offsprings than voles.

Random distribution pattern for *C. australis* found in this study may be a consequence of both population densities under carrying capacity and habitat characteristics, since coastal sand dunes are ecologically homogeneous habitats determining no concentration of animals in propitious patches. In contrast, uniform dispersion patterns were reported for other *Ctenomys* populations under high density conditions as well as in poor habitats (PEARSON et al. 1968; GALLARDO and ANRIQUE 1991; ROSI et al. 1992), whereas clumped distribution has been showed for *C. talarum* populations occupying grasslands with high plant biomass (MALIZIA 1994). HANSEN and REMMENGA (1961) have found displacements from clumped to uniform patterns in *Thomomys talpoides* with density increases.

The significant change in male to female ratio that occurs between new-born and adult *C. australis* indicates different mortality rates among sexes. Sex ratio skewed toward females suggests that this population is polygynous such that male-male aggression may play an important role in determining successful territory defense and access to multiple females.

Another source of mortality has been analysed for *C. australis*. VASALLO et al. (1994) found that only subadults were preyed upon by owls but the authors could not distinguish differences between sexes since no valid discrimination was obtained from pellet information. Thus, predation is more common than previously assumed for *Ctenomys* species although we have no information whether their incidence is uneven among sexes.

The studied population showed sexual bimaturism, females being the first to attain reproductive potentiality. An association between the degree of polygyny of a species' mating system and the extent to which males mature later than females has been reported (DALY and WILSON 1983). Since polygyny enhances male-male competition, it seems possible to interpret delayed maturity as a response to that competition.

Evidence for polygyny is reinforced from other sources. EMLEN and ORING (1977) predicted that in breeding systems where one male has exclusive access to multiple females, selection should cause the existence of sexual dimorphism in size. The more pronounced dimorphism in body weight than in length for *C. australis* may be attributed to the interplay between sexual and growth hormones leading to more robust males in comparison with females of similar length (BOONSTRA et al. 1993). Furthermore, a strong correlation exists between testes size and mating systems since its size is a consequence of copulatory frequency (SHORT 1977). Relative testes length found in this study for *C. australis* is still lower than the mean value reported for polygynous voles by HESKE and OSTFELD (1990). Thus, adult sex ratios skewed toward females (which could be considered an approximation of the operational sex ratio), sexual bimaturism, sexual size dimorphism both in weight and in length, and small relative testes size are all measures that allow to consider the studied population of *C. australis* as polygynous.

Since in *C. australis* the breeding season is continuous, it appears that photoperiod is not the cue that determines breeding in this species. For a subterranean rodent, composition and cover of plants would be a more reliable variable than photoperiod. In this sense, a detailed study on dietary preferences of *C. talarum* and *C. australis* (COMPARATORE et al. 1995) has revealed that *C. australis* is a herbivorous generalist feeding principally on the aerial fraction of vegetation with biomass in the grassland not differing between seasons.

Up to date, no information about production of secondary compounds from growing plants is known to stimulate reproduction in *Ctenomys* as was described for other rodents (ROWSEMITT and O'CONNOR 1989).

Continuous breeding determines the lack of a discrete period of recruitment as well as a complex age structure. This reproductive adaptation allows that more individuals were able to participate in matings, even young of the year, thereby moderating the potential effects of genetic drift that operates in populations where reproduction is over a short period.

Mean litter size of 2.9 reported here for *C. australis* is 30% lower than for *C. talarum* at two different localities (MALIZIA 1994). This situation could be related to grassland quality since plant cover where *C. talarum* inhabits is up to 80%. On the other hand, *C. mendocinus* (ROSI et al. 1992) shows the same litter size as *C. australis* and is distributed in xeric habitats with poor plant cover. Lower mean embryo counts for post partum pregnancies may be attributed to maternal care of the first litter, which limits the time and energy dispensability of the mother to collect plant material in a poor habitat, such as a sand dune.

Few studies exist dealing with direct quantification and characterization of dispersal of subterranean rodents (WILLIAMS and CAMERON 1984; RADO et al. 1992; MALIZIA et al. 1995; O'RIAIN et al. 1996). Nonetheless, more information has been provided by other authors which examined inferentially movements in this group of rodents (HOWARD and CHILDS 1959; VAUGHAN 1962; WILKS 1963; SMOLEN et al. 1980; PEARSON et al. 1968).

Recovery percentages reported here are nearly in the order of that found for *C. talarum* (MALIZIA et al. 1995) and *Geomys attwateri* (WILLIAMS and CAMERON 1984) and compares favorably only with the microtine *Microtus pennsylvanicus* (TAMARIN 1977) which presented the lowest dispersal rate among surface-dwelling rodents. This reflects an expected situation where low vagility appears associated with high local dependence of subterranean rodents to their local habitat.

Although male dispersal is proposed as a rule for mammals (Greenwood 1980), this pattern is not clear for subterranean rodents. Both sexes of *C. australis*, *G. attwateri*, and *C. talarum* from Necochea locality dispersed, whereas *C. talarum* from Mar de Cobo locality showed a predominance of males dispersing. This is a confusing result for *C. australis*, since the proposed polygyny may be associated with male dispersal. It is possible that the breeding system, mediated by the access to multiple females, would be responsible for dispersal of one part of the population (males), whereas for females, another source of resources, such as space, may be responsible for their mobility.

Previous experimental and inferential studies examining pocket gopher dispersal revealed that dispersers were usually young individuals. This situation fits the optimal dispersal theory for subterranean rodents (Nevo 1979, 1982) which predicts that once adults have established their territories, they will remain sedentary throughout their lives. This is not the case for *C. australis* in which, in spite of the absence of oldest individuals dispersing, the age structure of this group was a random sample of the resident population. Nonetheless, this dispersing group is characterized by being predominantly non-breeding individuals. The same trend was found for *C. talarum* (Malizia et al. 1995).

This characterization shows that dispersers are individuals leaving their natal site driven by the lack of resources that insure successful reproduction.

The fact that one part of the population disperses before reproduction has been proposed as a mechanism for avoiding inbreeding (Dobson 1982).

Apfelbaum et al. (1991) found moderate levels of genetic heterogeneity among four analysed populations of *C. australis*, where gene flow appears to play a significant role only in allowing the maintenance of a slight local differentiation. The ecological mechanisms that promote such a situation may be associated with the levels of vagility found in this study, coupled to both a random distribution pattern of individuals in a homogeneous habitat and the existence of a long breeding season. This determines both the lack of a discrete period of recruitment and the ability of more individuals participating in the reproductive process. All these factors contribute to make *C. australis* population relatively stable. In this sense, the persistence of these populations may depend strongly on the availability of propitious habitats according to its energetic and thermoregulatory restrictions. A previous study (Zenuto and Busch 1995) has demonstrated that *C. australis* mound-building and feeding activities maintain suitable habitats for themselves. Thus, it is important to control human land use in such a manner to guarantee the persistence of this special and vulnerable habitats.

Acknowledgements

Zusammenfassung

Populationsbiologie des unterirdisch lebenden Nagers Ctenomys australis (Tuco-tuco) in einem Dünenfeld an der Küste von Argentinien.

Die Populationsbiologie des unterirdisch lebenden Nagers *Ctenomys australis* (Tuco-tuco), wurde entlang eines Küstendünengebiets studiert. Die mittlere Populationsdichte lag in der beobachteten Periode bei 16.1 Ind./ha, wobei die Tiere eine zufällige räumliche Verteilung zeigten. Die Fortpflanzung erfolgte ganzjährig, was das Fehlen einer fest definierten Wurfperiode sowie eine komplexe Altersstruktur der Population bedingte. Das Geschlechterverhältnis war, bezogen auf die Gesamtpopulation,

zu den Weibchen hin verschoben, während es bei den Jungtieren ausgeglichen war. Weibchen erreich-
ten die Geschlechtsreife früher als die Männchen, hatten im Jahr ihrer Geburt aber nur einen Wurf. Im
Sommer war bei den Weibchen eine Überlappung von Schwangerschaft und Laktation zu beobachten,
wodurch die Existenz eines Postpartum Oestrus belegt wird. Die mittlere Wurfgröße betrug 2.9 Jung-
tiere, lag aber beim Postpartum Oestrus niedriger als bei der ersten Schwangerschaft. Die adulten Tiere
zeigten einen Geschlechtsdimorphismus hinsichtlich Gewicht und Größe. Bei den Männchen war eine
geringe relative Hodengröße zu beobachten. Dispersionen fanden, trotz überwiegend unterirdischer
Lebensweise, oberirdisch statt. Die monatliche Ersetzungsrate lag bei 19%, wobei die Besiedlergruppe
überwiegend aus nichtgeschlechtsreifen Tieren bestand. Zwischen Besiedlern und residierenden Tieren
konnten keine Unterschiede hinsichtlich Geschlechterverhältnis, Alterszusammensetzung und
Wurfgröße festgestellt werden.

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